ORIGINAL ARTICLES

The Effects of Seed Dispersal on the Simulation of Long-Term Forest Landscape Change

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ABSTRACT

The study of forest landscape change requires an understanding of the complex interactions of both spatial and temporal factors. Traditionally, forest gap models have been used to simulate change on small and independent plots. While gap models are useful in examining forest ecological dynamics across temporal scales, large, spatial processes, such as seed dispersal, cannot be realistically simulated across large landscapes. To simulate seed dispersal, spatially explicit landscape models that track individual species distribution are needed. We used such a model, LANDIS, to illustrate the implications of seed dispersal for simulating forest landscape change. On an artificial open landscape with a uniform environment, circular-shaped tree species establishment patterns resulted from the simulations, with areas near seed sources more densely covered than areas further from seed sources. Because LANDIS simulates at 10-y time steps, this pattern reflects an integration of various possible dispersal shapes and establishment that are caused by the annual variations in climate and other environmental variables. On real landscapes, these patterns driven only by species dispersal radii are obscured by other factors, such as species competition, disturbance, and landscape structure. To further demonstrate the effects of seed dispersal, we chose a fairly disturbed and fragmented forest landscape (approximately 500,000 ha) in northern Wisconsin. We compared the simulation results of a map with tree species (seed source locations) realistically parameterized (the real scenario) against a randomly parameterized species map (the random scenario). Differences in the initial seed source distribution lead to different simulation results of species abundance with species abundance starting at identical levels under the two scenarios. This is particularly true for the first half of the model run (0–250 y). Under the random scenario, infrequently occurring and shade tolerant species tend to be overestimated, while midabundant and midshade tolerant species tend to be underestimated. The over- and underestimation of species abundance diminish when examining long-term (500 y) landscape dynamics, because stochastic factors, such as fire, tend to make the landscapes under both scenarios converge. However, differences in spatial patterns, and especially species age-cohort distributions, can persist under the two scenarios for several hundred years.

Key words: seed dispersal; dispersal radii; dispersal probability; spatially explicit; landscape model; LANDIS; age cohorts; landscape pattern; fire disturbance; gap model; northern Wisconsin.

INTRODUCTION

The challenges in studying forest landscape change come from two fundamental aspects: the relevance of both long temporal and broad spatial dimensions. Temporally, forest ecosystems may take hundreds of years to undergo significant successional change. Factors that operate on such long time spans may go undetected by many commonly used field experiments. Such approaches often are based on rela-

tively short observation periods that may not capture the full range of stochastic events. Spatially, forest landscape change can be strongly affected for centuries by the heterogeneity of vegetation distribution at an initial point (Baker 1992; Wallin and others 1996; Foster and others 1997; He and Mladenoff 1999), which is in turn affected by variation in environmental conditions and resources. The interaction of spatial and temporal factors across the landscape is further complicated by interactive human and natural disturbances. Computer simulation modeling is a useful tool for understanding these large (10^4–10^6 ha), long-term, complex systems. With modeling techniques, it is possible to describe the modeled objects mathematically and logically and deduce results that cannot otherwise be investigated, especially at broad spatial and temporal scales (Turner and others 1995; Gardner and others 1999; Mladenoff and Baker 1999a).

Traditionally, forest landscape change has been modeled by simulating changes in sample plots of up to a few hundred square meters, selected within various forest types or along environmental gradients (for example, Pastor and Post 1988; Urban and others 1992; Fischlin and others 1995; Bugmann 1996). These models are often referred to as gap models (Botkin and others 1972; Shugart 1984; Pastor and Post 1985) and typically did not contain a high degree of spatial interactions among plots, or across a large landscape. The modeling results are often assumed to represent the much larger forest landscape within which plots are located. By using noninteracting plots, spatial complexity in ecological processes as well as spatial variation is ignored. Ecological processes occurring at spatial extents that cover hundreds or thousands of plots cannot be simulated with most gap models (Mladenoff and Baker 1999b).

Seed dispersal is an ecological process that interacts with landscape heterogeneity at broad scales. It can influence forest landscape change (Leishman and others 1992) because seed sources present on a given site can affect succession on surrounding sites within certain dispersal distance radii, varying by species seed characteristics and dispersal mode (Burns and Honkala 1990). Seed dispersal is often described with various mathematical distributions involving dispersal probability and seedling density (Portnoy and Willson 1993; Ribbens and others 1994; Kot and others 1996; Clark and others 1998). In gap models, large-scale, contagious processes, such as seed dispersal, usually have been assumed to be either constant or random (Shugart 1984). Recent models, such as FIRESUM (Keane and oth-

ers 1989), SORTIE (Pacala and others 1993, 1996), and FACET (Urban and Shugart 1992; Urban and others 1999), have incorporated more spatial interaction than the earlier JABOWA-FORET types of gap models. FACET considers interaction of directly neighboring plots when simulating seed dispersal (Urban and others 1999); SORTIE tracks individual tree locations and simulates seed dispersal by using mean dispersal distances and seedling density defined for each species (Ribbens and others 1994). But even with state-of-the-art computers, these new models are still limited to simulating relatively small sections of landscapes (for example, less than 10 ha; Pacala and others 1996; Caspersen and others 1999), because the computational loads increase exponentially with simulation area (He and others 1999b). To simulate large areas by using these models, spatially inexplicit scaling-up (for example, Acevedo and others 1995; Keane and others 1996; Urban and others 1999), or simplifying the representations of some ecosystem processes, are needed.

To study forest landscape change in landscapes larger than 10^4 ha, spatially explicit landscape models are needed that integrate broad-scale spatial and temporal processes. Landscape models are models that simulate large-scale ecological processes, such as seed dispersal, wind and fire disturbances, insect defoliation, forest disease, and harvesting. In this study, we illustrate how spatially explicit seed dispersal is simulated in LANDIS, a raster-based landscape model. We endeavor to examine how seed dispersal influences landscape change and how significantly the initial seed source abundance and distribution affects simulation results. We use both an artificial landscape and a large landscape (500,000 ha) in northern Wisconsin, USA to address these issues.

METHODS

LANDIS Model

Model Purpose, Scales, and General Dynamics. LANDIS is designed to simulate forest dynamics at large extents (10^4–10^6 ha), over long periods of time (for example, hundreds of years), by simulating individual species as 10-y age cohorts (Mladenoff and others 1996). LANDIS is a raster-based model in which cells or sites in a grid correspond to the plots or stands in gap models. Cell size can be varied from 10 to 500 m corresponding to a spatial scale that is considered appropriate for a given study and input data. A 500-y simulation of a 500×800-cell map with 23 species takes 1 h on a 940 MIPS (comparable to a Pentium Pro 400Hz PC) computer. Each site contains unique species, age cohorts, and envi-

Table 1.   Selected Species Life History Attributes Parameterized in LANDIS

Species	Long.	Matu.	ShadeT	FireT	EffD	MaxD	VegP	SpAge
Abies balsamea	150	25	5	1	30	160	0	0
Acer rubrum	150	10	3	1	100	200	0.5	150
Acer saccharum	300	40	5	1	100	200	0.1	240
Betula alleghaniensis	300	40	4	2	100	400	0.1	180
Betula papyrifera	120	30	2	2	200	5000	0.5	70
Fraxinus americana	200	30	4	1	70	140	0.1	70
Picea glauca	200	25	3	2	30	200	0	0
Pinus banksiana	70	15	1	2	20	40	0	0
Pinus resinosa	250	35	2	4	12	275	0	0
Pinus strobus	400	15	3	3	100	250	0	0
Populus grandidentata	90	20	1	2	−1	−1	1.0	90
Populus tremuloides	90	15	1	2	−1	−1	1.0	120
Prunus pensylvanica	30	10	1	1	30	3000	0	0
Quecus ruba	250	25	3	3	30	3000	0.5	250
Tsuga canadensis	450	30	5	3	30	100	0	0

Long., longevity (year); Matu., age of maturity (year); ShadeT, shade tolerance class; FireT, fire tolerance class; EffD, effective seeding distance (m); MaxD, maximum seeding distance (m); VegP, vegetative reproduction probability; SpAge, maximum age of vegetative reproduction (year).

ronmental information. For each site, individual species are recorded as presence/absence of 10-y age cohorts. This provides explicit seed source information. The model is made up of three general parts: landscape scale ecological processes, site or plot scale ecological processes, and environmental data layers characterized by landtypes that stratify a heterogeneous landscape into relatively homogeneous units. Landscape scale processes include seed dispersal, fire and windthrow disturbances, insect defoliation, and forest harvesting. Site scale ecological processes include forest successional dynamics for individual species (age class presence/absence), such as seedling establishment, species regeneration (birth), growth, death (when reaching longevity), random mortality, and vegetative reproduction. Landtypes are further grouped into active and nonactive. The latter contains nonforested sites, such as water, lowland, and other nonforested classes that are not simulated by LANDIS.

Further information on LANDIS overall model design (Mladenoff and others 1996), model assumptions and behavior (Mladenoff and He 1999), fire disturbance (He and Mladenoff 1999), species and age-list objects (He and others 1999b), model calibration and result verification (He and Mladenoff 1999), and model parameterization (He and others 1996) can be found elsewhere.

Seed Dispersal and Seedling Establishment Dynamics.

In LANDIS, the available seed source locations (cells with tree species) and ages are precisely defined. Seed dispersal and seedling establishment processes are simulated as several steps: dispersal,

light condition checking, and site condition checking (Mladenoff and He 1999). Light and site conditions affect establishment after dispersal. For any species, seed dispersal distance is modeled as a function of its effective and maximum seeding distances. Effective seed dispersal distance is that for which seed has the highest probability (for example, $P > 0.95$) of reaching a site. The maximum seed dispersal distance is that distance beyond which a seed has near zero probability (for example, $P < 0.001$) of reaching. These distances are derived (Table 1) from previous literature for various tree species (for example, Loehle 1988; Burns and Honkala 1990). Seed dispersal probability (P) between the effective (ED) and maximum seeding distance (MD) follows a negative exponential distribution:

$$P = e^{-b \cdot (x/MD)} \tag{1}$$

where x is a given distance from the seed source (MD > x > ED), MD is the maximum seeding distance, and b is an adjustable coefficient ($b > 0$), which can change the shape of the exponential curve corresponding to various seed dispersal patterns when information is available (Figure 1). If $x \leq$ ED, we set $P = 0.95$, indicating that the probability of seed dispersing within its own effective seeding distance is very high, while if $x \geq$ MD, we set $P = 0.001$, indicating that the probability of seed dispersing beyond its own maximum seeding distance is very low.

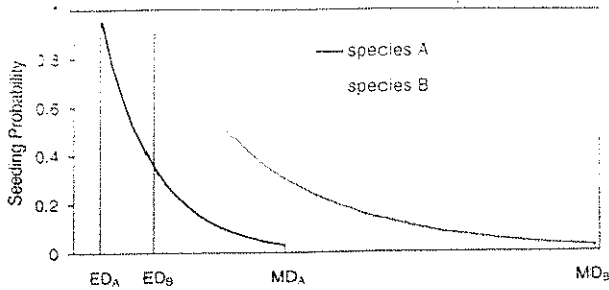When seed successfully arrives at a given site, the light condition checking procedure determines

Figure 1. The negative exponential distribution of tree species seeding probability in relation to distance from available seed sources. ED, species effective seeding distance; MD, species maximum seeding distance.

whether seedlings are allowed to establish based on the shade tolerance rank of the seeding species relative to the species already occurring on the site. For example, paper birch (*Betula papyrifera*) is a shade intolerant species that cannot seed into a site on which hemlock (*Tsuga canadensis*) is already established. When light conditions are favorable to a species, the site condition checking procedure determines if the species can establish (Mladenoff and He 1999). The environmental conditions of a site, such as soil nutrient and water availability, may favor certain species over others. The species establishment coefficient, a number from 0 to 1, is introduced in LANDIS as a relative scaling of how environmental conditions favor various species (Mladenoff and others 1996). These factors are not mechanistically simulated. Rather, they are assigned probabilities that can be derived empirically or from the simulation results of an ecosystem process model (He and others 1999a).

Fire Disturbance. Disturbance is simulated in combination with successional dynamics. Fire is simulated as a stochastic process based on the distribution of fire return intervals and fire sizes, derived from existing or historical data (for example, for the northern U.S. Lake States, Heinselman 1973, 1981; Frelich and Lorimer 1991; Baker 1992). The distribution of fire sizes and fire return intervals are characterized for all landtypes within a simulated landscape (He and Mladenoff 1999). Dry, sandy landtypes experience fire more frequently than mesic landtypes. LANDIS simulates fires of five classes, reflecting fires of low (ground fires) to high intensity (crown fires). Tree species are grouped into five fire tolerance classes. Small, young trees are assumed to be more vulnerable than large, old trees. Fire severity is the interaction of susceptibility (species age classes), species fire tolerance, and fire intensity, which is determined by the time since last fire, a surrogate for the amount of fuel. Fuel accumulation

regimes also differ by landtypes, reflecting variability in production and decomposition rates (He and Mladenoff 1999).

Test Landscapes

First, to illustrate how seed dispersal is simulated in LANDIS, we use an artificial landscape containing four isolated tree seed sources of different species. Next, to demonstrate the effects of incorporating spatially explicit seed source information across a landscape, we will use an actual landscape and compare the simulation results of landscape change and species abundance based on two seed dispersal scenarios under a natural fire disturbance regime.

1. A landscape with spatial distributions of seed sources (tree species) as they occur on a real landscape, referred to as the real scenario;

2. The same landscape with spatial distribution of seed sources in the same proportions as the real scenario, but randomly distributed across the landscape, referred as the random scenario.

Artificial Landscape. A square artificial landscape was designed containing 10,000 cells (100×100 grid cell) with cell size equalling 20×20 m. Mature sugar maple (*Acer saccharum*), hemlock, white pine (*Pinus strobus*), and red oak (*Quercus ruba*), at age cohorts of 50 y, are set at the four corner cells, respectively (Figure 2). The rest of the landscape is open land for seed dispersal and seedling establishment. To minimize variations that affect seed dispersal, we let the entire artificial landscape contain one landtype, and species establishment coefficients of the four species are the same (0.5). We simulated the landscape up to 200 y. At this point nearly all of the open areas were covered by the simulated species.

Real Landscape. The real landscape we simulated represents approximately 500,000 ha located in northern Wisconsin (44° N, 91° W), USA. The area has very little topographic relief. Upland forests cover approximately 60% of the landscape with more forest cover in the north. Lakes and lowlands are scattered on the landscape, occupying 5.2% and 7.5% of the area, respectively. Other nonforest categories, such as croplands and pastures, occur on 27.7% of the landscape. Forests are somewhat fragmented, particularly in the south, due to the large proportion (40%) of nonforest categories and historical logging (Mladenoff and Pastor 1993). Nonforest categories are not simulated by LANDIS and remain static throughout the simulation. This is an environmentally heterogeneous region and was quantitatively classified into six relatively homogeneous landtypes based on soil and climate variables
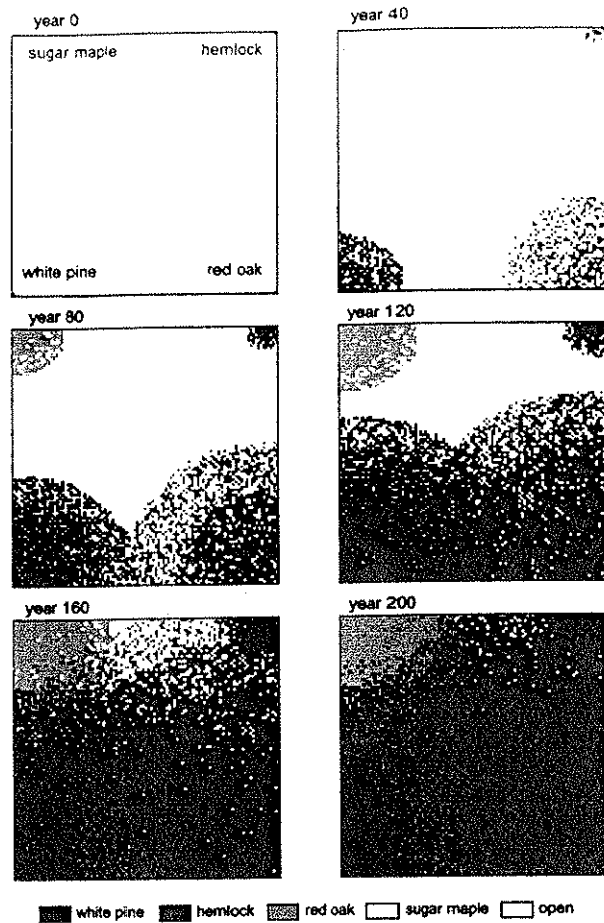
Figure 2. Demonstration of seed dispersal patterns of four tree species on an artificial landscape: sugar maple, hemlock, white pine, and hemlock at year 0, 40, 80, 120, 160, and 200. The corner cells at year 0 represent the starting point for each species.

(Host and others 1996). More details on the study area can be found in He and Mladenoff (1999).

We divided the study area into a 4,854-km² grid containing 121,362 cells (358×339) with a 200×200-m cell size. Forest composition and age information of the study area were parameterized at the individual species level (presence of 10-y age cohorts), from classified Landsat satellite thematic mapper (TM) imagery (Wolter and others 1995) and forest inventory data, by using a method described by He and others (1998). This provides the explicit location and age classes of seed sources, for example, hemlock (see Figure 6a).

Random Landscape. For the random scenario, we kept the distribution of nonforest classes unchanged and randomized the distribution of each of these species based on the existing species maps. These new maps preserve the proportion of the species

and their age classes on the landscape and higher level landscape structure, such as upland forest, nonforest, water, and wetlands, with randomized locations of the distribution of seed sources within forest areas, such as shown for the hemlock (see Figure 6b).

Simulation Controls

We merged the six landtypes present in the study area into a single landtype for the real and random scenarios. This minimizes the differences caused by factors other than seed source distribution and seed dispersal, such as environmental variation at the broadest scale. Fine scale heterogeneity due to initial landscape structure, such as forest vs nonforest is retained. All simulations were conducted under a natural fire disturbance regime with mean fire return interval of 800 y and fire severity of class 5. Because class 5 fires are the most severe, they can spread while ignoring the vegetation differences under the real and random scenarios. Fires are stochastic. Neither the time of occurrence nor the fire size is repeatable for a given fire. We set the same random number seed (a model input parameter) for different runs. Therefore, the randomly generated disturbance regimes (individual fires) are identical in both the real and random scenarios (He and others 1996). This ensures that the stochastic results from real and random scenarios were comparable. All simulation results were calibrated to ensure that the proposed fire disturbance regimes were correctly simulated (He and Mladenoff 1999)

Simulated species abundance and distribution for a given time step involves stochasticity such as fire events; therefore we compare all simulation maps and mean abundance derived from the time span of the simulations (50 time steps total). Individual species abundance at every 10-y time step was calculated as the percentage of cells in the active landscape containing a given species. Mean abundance was then calculated as the average abundance from these individual time steps over the period of simulation. For the random scenario, we calculated percentage of error of the mean abundance against the real scenario as the standard according to the following equation:

$$\% \text{ error} = (\text{random mean} \qquad (2)$$

$$- \text{real mean})/\text{real mean}) * 100$$

Positive numbers indicate the overestimation of species abundance in the random scenario, while negative numbers indicate the opposite.

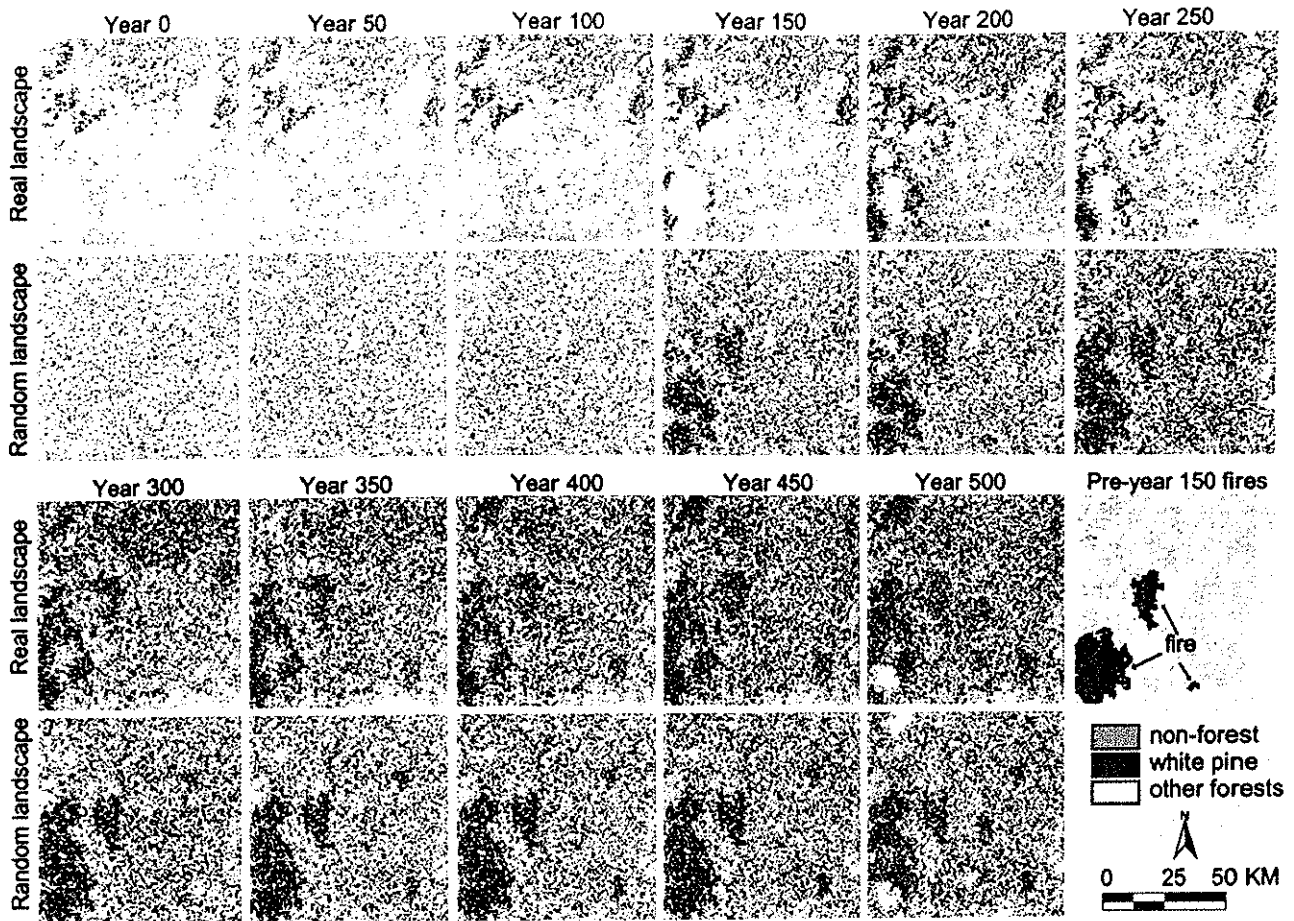Figure 3. Dynamics of white pine simulated under real and random scenarios from year 0 to 500.

RESULTS

The Artificial Landscape

With uniform environmental conditions, species dispersal and establishment on the artificial landscape is mainly a function of species seeding capabilities as defined by their effective and maximum seed dispersal distances and relative age to sexual maturity. The seedling establishment patterns reflect the seeding probabilities defined in Eq. (1) (Figure 1), where areas close to a seed source of given species are more densely covered by the species than areas further from the seed source. These gradients are obvious from year 40 to year 80 (Figure 2). Species with larger maximum seeding distances (such as red oak, which can be dispersed at low density but long distance by birds) progressed more rapidly than the other three species. Red oak has the greatest dispersal radius but variable probability at the maximum distance (Figure 2). With the artificial landscape, spatial patterns of different species reflect their seed dispersal radii especially before year 120

(Figure 2). As expected, hemlock, with the shortest effective and maximum seeding distance, made the least progress through the 200-y simulation (Figure 2). This implies that available seed source on the landscape is important to hemlock abundance due to its relatively low dispersal ability. The seeding distances of sugar maple are longer than that of hemlock, resulting in a higher cover of sugar maple than hemlock on the landscape. White pine has the same effective seeding distance and similar maximum seeding distance as sugar maple, but it dispersed much faster than sugar maple. This is because white pine has the lowest sexual maturity age (15 y) among the four species (Table 1). The newly dispersed white pine age cohorts mature more quickly than the other species, and they can serve as many new seed sources, which in turn increase white pine abundance on the landscape.

As observed from year 120 to 200 in the simulation, seed dispersal also was affected by the species relative shade tolerance and competition. The simple circular patterns of species distribution driven by

seed dispersal radii are obscured where the radii of different species overlap and species competition occurs. Such effects were found especially for both white pine and red oak at years 120, 160, and 200 (Figure 2). At year 200, the formerly open landscape was almost completely occupied by forest. White pine and red oak seeds cannot establish in areas where hemlock and sugar maple already exist. However, hemlock and sugar maple, the more shade tolerant species, will continue to disperse under white pine and red oak. In the absence of fire, they will eventually outcompete white pine and red oak on this landscape (results not shown). New and complex patterns can be formed from the interactions of other factors interacting with seed dispersal, as will be shown below.

Real Scenario vs Random Scenario

For real landscapes, multiple locations can be found as seed sources for any given species. Overlap of species dispersal radii is common. The interactions of species competition and disturbance, plus the percentage of nonforest areas that often serve as barriers for seed dispersal, make it unlikely to observe species establishment patterns being driven simply by seed dispersal radii. Competition under the real scenario, where the landscape is fully occupied, complicates the impact of seed dispersal on species migration compared with the artificial landscape. In this study, we are able to trace the spatial dynamics of a given species over the period of simulation. In the simulation shown in Figure 3, we chose white pine, a dominant forest species before European settlement but occurring only on approximately 6% of the forested landscape today.

At the beginning of the simulation (Figure 3), white pine was largely distributed in the northern part of the study area and occurred only sparsely in the south due to historical disturbance and environment constraints. Because we assumed a homogenous environment for the entire landscape, white pine migration south is expected. As simulated, the migration of white pine is a gradual process that interacts with disturbance, seeding, and competition (Figure 3). Although white pine has early maturity and great seeding ability, as shown on the artificial, open landscape (Figure 2), its seedlings cannot establish on sites already occupied by shade tolerant species, such as sugar maple and yellow birch, which are common in this area. A relatively stable state for white pine prevails for approximately the first 100 y until the forest ages. During this period, there is a gradual accumulation of fuel, and the fire probability increases. A significant fire occurs at year 120 (Figure 3), creating open space by

removing shade tolerant species, thereby favoring white pine establishment. However, a large, severe fire can also reduce white pine abundance, benefiting less shade tolerant species, such as paper birch and aspen. A spatially explicit seed source is important for species colonization after fires, as shown by the small white pine patches that occur at year 150 in the south where the 120-y fire occurred (Figure 3). White pine encroachment into the open space takes approximately 200 y, and it is largely colonized at around year 300. The initial white pine patches in the north are thinned by fires and eventually broken down to relatively small patches, while new, younger patches formed after fire disturbances in other parts of the landscape from year 250 to 500 (Figure 3).

In the random scenario, white pine abundance before year 150 is slightly higher than in the real scenario, and white pine distribution is fairly stable (Figure 3). The same fire that occurred in the real scenario at year 120 also occurred under the random scenario, as a result of the fixed random number seed (He and others 1996). With maximum area covered by seed dispersal radii under the random scenario, white pine colonizes the open space created by this fire in approximately 100 y (year 150–250), much faster than the time needed in the real scenario (Figure 3). Because the overall abundance of white pine on the landscape is relatively low, these spatially explicit dynamics are not reflected in the white pine abundance trajectory (Figures 3 and 4d). From year 250 to 500, white pine abundance remains relatively stable, with a few small fires occurring on the landscape, causing maps from real and random scenarios to converge (Figure 3)

The random scenario immediately maximizes the area that seed dispersal radii cover, and results in some of the largest possible increases in a species abundance over time. This is seen from the percentage of error estimates for most species, especially for the first 250 y (Figure 4), indicating the increasing divergence between real and random scenarios. However, as the runs continue, this difference gradually decreases (Figure 4), and the percentage of error estimates are lower than in the first half of the simulation (discussed later). For the first half of the model run, the highest overestimates in the random scenario (average percentage of error across 0–250 y) are found for the least abundant species (Figure 5), such as hemlock (17.4%), jack pine (36.0%), red pine (11.5%), and white pine (4.1%). Overestimates in the random scenario for the abundant and shade tolerant species are low (for example, sugar maple 0.6%, the lowest among all species). These overestimates decrease during the
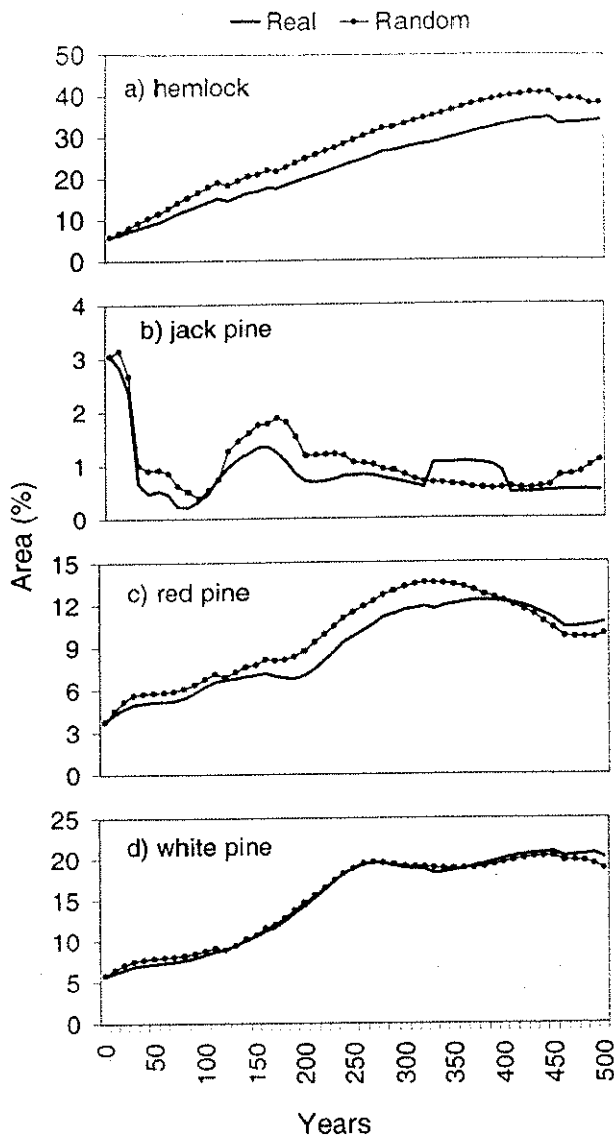
Figure 4. Simulated abundance for (a) hemlock, (b) jack pine, (c) red pine, and (d) white pine under real and random seed source distribution scenarios.

Figure 5. Percentage of error of species abundance in the random vs real scenarios calculated as [(random-real)/real * 100] across 500-y simulation. Positive numbers indicate an overestimation of species abundance under the random scenario; negative numbers indicate an underestimation.

second half of the model run (250–500 y; Figure 5), with hemlock (16.6%), jack pine (17.2%), red pine (3.9%), and white pine (−1.1%). Negative percentage of error indicates an underestimate under the random scenario. Underestimates occur for mid-shade tolerant, midabundant species, such as yellow birch (*B. alleghaniensis*) and red oak in the random scenario (Figure 5). Red oak was underestimated (−0.9%) from year 0–250, as were yellow birch (−3.4%) and paper birch (−3.7%). These underestimates increase from year 250 to 500 with red oak (−16.5%), yellow birch (−8.1%), and paper birch (−13.9%) (Figure 5). For less abundant, shade intolerant species, such as jack pine, species abun-
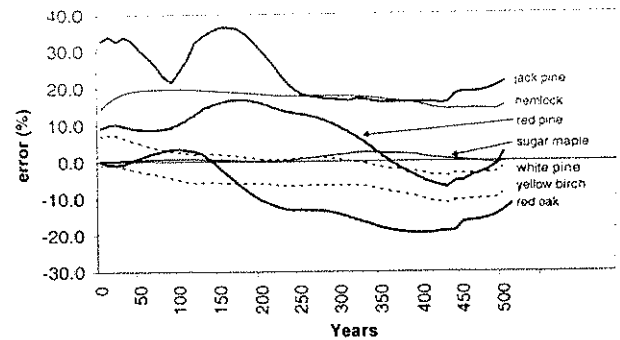
dance is more variable under the real scenario than that under the random scenario.

The difference between the two scenarios becomes more obvious when examining species age-cohort distribution. For example, hemlock, historically a dominant species in this area, is young and not common, with the majority around 30–60 y old (Figure 6a). It is distributed as a few large patches in the north and scattered seed sources in the south (Figure 6a). This spatial structure was randomized (Figure 6b). It is interesting to note that hemlock distribution in the south is very similar on both landscapes (Figure 6a and b). At year 200, the spatial patterns become very similar in the south on both landscapes due to stochastic fire disturbance and the similar starting conditions (Figure 6c and d). However, the initial, young hemlock patch in the northeastern area has succeeded into a large old-growth patch approximately 210 y old (Figure 6c). These patterns are not reflected in the random scenario.

DISCUSSION

Simulation Approach Implications

Tree species seed dispersal curves lead to a circular-shaped species distribution pattern on the artificial landscape. Because LANDIS simulates at 10-y time steps, this pattern reflects an integration across annual variation and possible dispersal shapes and establishment that might be caused by the variation in climate and other environmental variables (Houlé 1998). Shapes of seed dispersal probability curves are affected not only by dispersal distances but also by the coefficient b (Eq. 1), which currently is a constant ($b = 1.0$) in LANDIS. However, various species may be more specifically described with
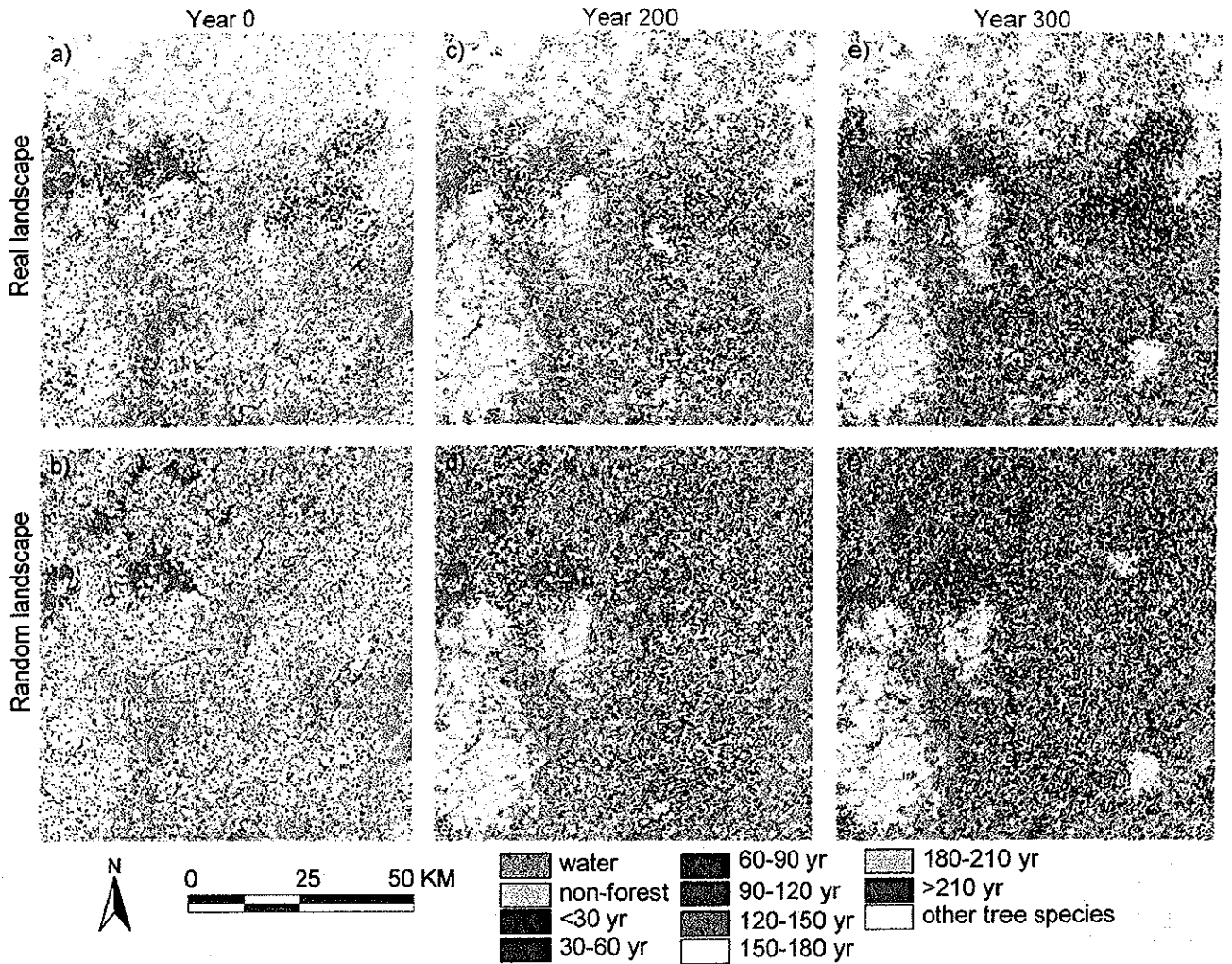
Figure 6. Hemlock seed sources distribution and spatial pattern under the real and random scenarios at (a) and (b) year 0, (c) and (d) year 200, (e) and (f) year 300, respectively, illustrating that the initial difference of seed source distribution on the landscape can last several hundred years.

dispersal curves of different shapes (Portnoy and Willson 1993). It is feasible for LANDIS to further parameterize b by species when the information is available. Under the real scenario simulation, seed dispersal pattern is modified and obscured by species competition, natural and human disturbance, and variation in environmental conditions (not simulated in this study) can significantly change these underlying patterns. Therefore, verification and understanding of seed dispersal patterns for each individual species is important.

It is relevant to point out that results from LANDIS simulations are semiquantitative. That is, because only species age-cohort presence/absence is tracked, not individual trees, forest density is not incorporated. Therefore, the actual number of seeds per unit area of a species arriving at a given site is

not simulated as can be done in other models that track individual trees (for example, Ribbens and others 1994). Investigations representing seed density at large, spatial scales pose challenges and warrant further study. Nevertheless, the results of our study reveal, to an extent, forest ecological dynamics incorporating spatially explicit seed sources on large landscapes.

Effects of Seed Dispersal on Species Abundance

A spatially explicit description of a species seed source is essential in forest landscape change studies, because each seed source can potentially affect the successional dynamics of its surrounding sites within its species dispersal radius. Our simulation results indicate that there is over- and underestima-

tion of species abundance under the random scenario, in comparison to the real scenario. For the first half of the simulation (0–250 y), there is increasing species abundance for less common species, such as hemlock and pine. This is because seed source abundance is the most limiting factor, and the random scenario maximizes the total area that these species dispersal radii cover. For some midabundant and midshade tolerant species, such as yellow birch and red oak, the random scenario produced lower abundances than the real scenario. For these species, competition rather than seed source abundance becomes a primary factor determining their abundances. Because red oak and yellow birch cannot establish on sites where hemlock resides, their abundances decreased in the second half of the simulation especially while hemlock increased to approximately 30% of the landscape during the second half of the simulation under the random scenario (Figure 4a)

Spatial Impacts of Seed Dispersal

The initial spatial patterns, due to legacies of past land use significantly influence subsequent forest landscape succession. For example, spatial differences simulated under the real scenario and random scenario for white pine (Figure 3) and hemlock can persist for several hundreds of years. This observation agrees with results of others (for example, Baker 1992; Wallin and others 1996; Caspersen and others 1999). Hence longer simulations make starting conditions less important due to disturbance and other stochastic events. The impact of initial species distribution patterns can be extended through seed dispersal as shown with hemlock. As the initial cohorts of hemlock age reach sexual maturity and produce seed, new cohorts occur around these initial cohorts (Figure 6).

At the end of the 500-year simulation, landscapes under both real and random scenarios converge significantly, as seen for white pine (Figure 3) and hemlock (Figure 6). The reasons for the resemblance are twofold. First, in this landscape, fire disturbance is the dominant factor shaping landscape pattern. With 800-y mean fire return interval, approximately two-thirds of the landscape is disturbed on both landscapes during a 500-y simulation, leading to the expected convergence of the two landscapes after several hundred years. Conceivably, with shorter mean fire return intervals, landscapes under random and real scenarios may converge sooner. Second, in our study area, with approximately 40% of the area in nonforest, the forest landscape is highly fragmented, and the real

species distribution patterns do not differ significantly from the random scenario as much as is possible in a more nonfragmental landscape. Therefore, the area covered by seed dispersal radii in both scenarios does not differ greatly for many species, and the final species abundances for the entire study area are fairly close under real and random scenarios.

Because detailed species and age information necessary for the parameterization of individual cells is not often available at landscape scales, the random scenario is often used (for example, Shifley and others 1997). Our results suggest that use of a random seed source scenario can be valid when (a) examining long-term (several hundred years, given longivity of the species here) forest landscape changes; and (b) simulating with relatively short mean fire return intervals in relation to species life spans.

CONCLUSION

Species migration is a large spatial (10^4–10^6 ha) and temporal scale (10^2–10^3 y) process (Davis and others 1986; Pitelka and the Plant Migration Workshop Group 1997, Clark and others 1998). Such processes occur in a spatially explicit manner through seed dispersal. The influence of seed dispersal will directly affect species abundance and composition as well as migration rates across the landscape. In simulations not incorporating seed dispersal, species abundance on a landscape remains constant until either species reach their longevity and die or the landscape is altered by disturbances. Spatially explicit landscape models simulating seed dispersal mechanistically can lead to more accurate assessments of how species may migrate across real, structured landscape than nonspatial approaches.

Both species abundance and the spatial structure of its initial distribution (presence/age) have significant impacts on sequential changes of forest landscapes. This is particularly true when examining forest landscape dynamics at relatively short time spans (for example, less than 10^2 y). Although the influence of initial conditions declines over time, it can remain apparent for hundreds of years, especially for long-lived species, such as hemlock, with low seed dispersal capability.

Use of unrealistic initializations of species abundance and distribution can cause over- and underestimation of species abundance, which depend on simulation time span, disturbance frequency, and

landscape configuration (not directly addressed in this study). A randomly parameterized species distribution may be used to examine forest landscape change when simulation spans are longer than species longevity and mean return intervals of the major disturbances, such as fire. In addition to random species distribution, unrealistically assigned initial species age distribution and the impacts of environmental heterogeneity, may further obscure the effects of seed dispersal, and warrant further investigation.

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